LXXII.—*A Contribution to the Knowledge of the Genealogy and Classification of the Crustacea.* By Prof. Karl Grobben, of Vienna *.

A constant attraction towards fresh consideration in respect of phylogeny is exerted by the Crustacea, a class presenting a variety of form and withal sharply defined, and which in Fritz Müller's treatise 'Für Darwin' (Leipzig, 1864), which has become famous, first served as a test of the correctness of the Darwinian theory. It was to such a consideration that I subjected the group on the basis of ideas which I have pursued for a number of years.

As the starting-point for my reflections I availed myself of the striking fact, as to which doubts have been expressed in isolated cases only †, that the large Phyllopods, which I shall henceforth designate as Euphyllopoda, and which among existing Crustacea come nearest to the ancestral forms of which they may be regarded as remnants, are represented by three types. These are *Branchipus*, *Apus*, and *Estheria*, which, while agreeing in all essential structural characters, differ very widely one from another in outward appearance as a whole, as well as in the special form of the several parts of their bodies.

On the other hand, it struck me that among the Euphyllopoda certain points of agreement with the Malacostraca are especially exhibited by *Branchipus*, while the type of which

* Translated from the 'Sitzungsberichte der kaiserlichen Akademie der Wissenschaften.—Mathematisch-naturwissenschaftliche Classe,' ci. Bd. ii. Heft, Jahrg. 1892, Abth. i. pp. 237–274: Wien, 1892.

† Thus it is considered by A. S. Packard that the large Phyllopods are a highly developed and extremely specialized branch of the Cladoceran stem, which is further connected by means of the Ostracods with the Copepods, from which it must be held to have been derived ('A Monograph of the North-American Phyllopod Crustacea,' United States Geological and Geographical Survey, Washington, 1883, pp. 417, 419, and 448).

Moreover, G. O. Sars ('Report on the Phyllocarida collected by H.M.S. 'Challenger' during the years 1873–76,' Zoology, vol. xix., 1887) regards the Copepods as the most primitive of recent Crustacea, and derives the Branchiopods from Copepod-like ancestors. In a similar manner Hartog ("The Morphology of *Cyclops* and the Relations of the Copepoda," Trans. Linn. Soc. Lond. ser. ii. Zoology, vol. v., 1888) considers the Copepods to be a primitive type and the ancestral form of the Crustacea. It was not until a later stage in the series that, according to Hartog, the Protophyllopods were derived from a Copepod-like ancestral form of this kind; the Protophyllopods on their part gave rise on the one hand to the Phyllopods, and on the other, through the Nebaliids, to the Arthrostraca and Thoracostraca.

Apus is an example is to be found in the Copepoda and in their allies the Cirripedia; and that the Ostracoda in many respects exhibit characters of *Estheria*, not to speak of the Cladocera, whose close affinity to *Estheria* will not be disputed.

In addition to this there came the conviction that the present grouping together of the lower Crustacea as Entomostraca, as opposed to the Malacostraca, does not betoken a natural arrangement.

All these points led me to inquire whether, as a matter of fact, *Branchipus* ought not to be regarded as a remnant of the Archi-Phyllopod series, from which the Malacostraca have sprung, while a similar remnant is represented by *Apus* in the case of Copepods and Cirripedes, and by *Estheria* in that of the Ostracoda, and at all events in all probability of the Cladocera; and whether, in the event of an affirmative answer to this question, an attempt should not be made to establish a more natural system of classification among the Crustacea composing the group Entomostraca.

In discussing this question we shall in the first place have to compare one with another the three Euphyllopod types above mentioned, as well as the peculiarities of the different Crustacean orders. For the purposes of such a consideration it will suffice to institute a comparison between merely the most primitive forms in each individual order.

As regards the structure of the Crustacea material is available in abundance in the shape of a voluminous literature, which, however, I do not intend to quote in full in this paper; in the present communication only a certain number of publications will be cited, and in the first instance such as demand closer consideration with reference to my views.

The Euphyllopoda.

Among the Euphyllopoda the *Branchipus*-type appears to be the most primitive, although again many of its peculiarities must be regarded as having been secondarily acquired. Among the primitive characters must be mentioned the elongated form of the body, the fin-like development of the furca, which is beset with setæ along its entire margin, the situation of the eyes upon stalks, the similar development and the form of the thoracic appendages, and the prolongation of the heart throughout the whole of the body-segments; on the other hand, a secondary character is seen in the absence of a shell, which originally must also have been present in the ancestors of *Branchipus*; of a secondary nature again is the smaller

number (20)* of the segments of the body as compared with what we find in *Apus* and *Estheria*, the sharp separation between the thoracic and the abdominal region, the latter of which is devoid of appendages in the adult, and the modification of the second antenna into a lamelliform structure in the female and into an apparatus of considerable size in the male. By the absence of the shell, the elongated form of the body, the powerful development of the musculature of the trunk, which comes into action in the darting motion of the body, and the not very large number of segments in the thorax and abdomen, *Branchipus* is characterized among the Euphyllopoda as the form best adapted to the movement of swimming.

On comparing *Apus* with *Branchipus* the first point which will have to be noticed as a primitive character in the case of the former is the larger number (33) † of the segments of the body. In *Apus*, too, the transition from the thorax to the limbless abdomen appears to be a more gradual one, owing to the fact that there is a continuous and very striking diminution in the size of the thoracic appendages towards the rear. As a peculiarity which is found in *Apus* alone among the Euphyllopoda must be mentioned the large number (63) of the thoracic appendages; the eleven anterior segments of the body each bear one pair of appendages (they correspond to the eleven limb-bearing thoracic segments of *Branchipus*), while upon the following seventeen segments we find a larger and posteriorly increasing number of limbs, so that to the last two limb-bearing segments there together belong twelve pairs of appendages. I will not here attempt to decide whether in the posterior section of the thorax of *Apus* we have to deal with a fusion of several segments to form larger annuli, or with a multiplication of the appendages within the segments, although I rather incline to the latter view. In any case, whether concentration of segments or multiplication of the appendages has taken place, it would be a question of a secondary condition.

Thus, should the actual number of the body-segments be determined by the number of the appendages, the segmentation of the body, in this case unusually extensive, would surely have to be regarded as a secondary character.

Apus bears a small shield-shaped shell covering the anterior segments of the thorax, and herein possesses, as opposed to *Branchipus*, an old character belonging to the common

* Among the Branchipodidæ the genus *Polyartemia* alone possesses a larger number of segments (namely 22), nineteen of which bear appendages.

† The numbers refer to *Apus cancriformis*.

ancestral form. The lateral margins of the shell in *Apus* are directly continuous with the anterior border of the head, a peculiarity to which we shall have to revert later on. Divergence from the original ancestral form is seen in the special development of the thoracic appendages. As opposed to *Branchipus*, in which the appendage is expanded like a leaf, we find in *Apus* a narrow elongated axis and an elongated stiff form of endites, the most distal of which (the sixth) corresponds to the endopodite*. It is true that this elongated form is in the first instance assumed only by the anterior appendages, while the posterior ones are very broad. Yet in my opinion the anterior limbs of *Apus* (although not exactly the two first, which have undergone further modification) exhibit the more primitive form with reference to the shape of the larval limbs, and also with regard to the form of the appendages which must be assumed for the ancestral types.

The furcal appendages in *Apus* are elongated and developed into the shape of filaments. As a secondary character must be regarded the total loss or the far-reaching degeneration of the second antenna, the original function of which as a swimming-foot has been taken over by the first thoracic appendage, which is furnished with long flagelliform processes. The heart does not extend, as in *Branchipus*, throughout the whole of the segments of the body, but is confined to the anterior half of the trunk, a phenomenon which, when contrasted with the primitive condition met with in *Branchipus*, must be regarded as of a secondary nature. In a similar fashion is to be interpreted the displacement of the compound eye in *Apus*. The two eyes are not situated upon stalks, but, as I have previously shown †, are sunken and covered by a reduplicature of the skin ; at the same time they are closely approximated to the median line.

A type which in general appearance diverges very widely from *Branchipus* as well as from *Apus* is constituted by *Estheria*. In this case the body is thickset and laterally

* I am unable to assent to the interpretation given by Ray Lankester ("Observations and Reflections on the Appendages and on the Nervous System of *Apus cancriformis*," Quart. Journ. Micr. Sci. vol. xxi., 1881, p. 363) of the sixth endite as the exopodite, and of the fifth as the endopodite, since the facts of embryology go to show that the sixth endite corresponds to the endopodite and the flabellum to the exopodite.—*Cf.* C. Claus, "Zur Kenntniss des Baues und der Entwicklung von *Branchipus stagnalis* und *Apus cancriformis*," Abhandlungen der königl. Gesellschaft der Wissenschaften zu Göttingen, xviii. Bd., 1873, p. 20.

† *Cf.* C. Grobben, "Die Entwicklungsgeschichte der *Moina rectirostris*. Zugleich ein Beitrag zur Kenntniss der Anatomie der Phyllopoden," Arbeiten des zoolog. Institutes zu Wien, Bd. ii., 1879, pp. 51 *et seq.*

compressed, while together with the head it is completely covered by the ample bivalve shell, which is closed by a muscle. The number of the segments of the body is larger than in *Branchipus* (amounting to as many as 28), and the elongate lamelliform appendages appear on all the free thoracic segments, gradually diminishing in size towards the rear. The end of the abdomen exhibits a very peculiar development and is seen to be bent towards the ventral surface and cleft into two lamellæ, which are armed at the end with hook-shaped furcal branches. A decidedly ancient character is to be observed in the second antenna, which has retained the shape of a swimming-foot. The heart remains still shorter than in *Apus*, and merely extends through the foremost portion of the body. The two compound eyes are in complete contact one with another in the median line; at the same time, just as in the case of *Apus*, they are sunken and overgrown by a reduplicature of the skin. While, however, in the case of *Apus* the eyes are driven to the dorsal side, in consequence of the lateral extension of the carapace and the inclusion of the head in its prolongation, we find them in *Estheria* enclosed in the narrow head, above and beyond which lie the valves of the shell. The peculiar position of the two eyes, as well as their convergence in the median plane, is occasioned by the formation of the shell, as has already been explained by Dohrn *. In consequence of the inclusion of the body between the valves of the shell and the lateral compression connected therewith the original eye-stalks degenerated and the eyes were pressed together in the median line. The opacity of the shell favoured this process. The overgrowth of the fused eyes by the skin may have developed as a protection for the visual organ in connexion with the burrowing mode of life of *Estheria*, just as the same cause probably cooperated in the case of *Apus* also. It is probable that the overgrowth and approximation of the eyes in *Apus* and *Estheria* arose independently in the two groups.

As a secondary character which is common to all three Euphyllopod types must be mentioned the degeneration of the mandibular palp and the reduction of both pairs of maxillæ.

The peculiar development of the furca and the relative heaviness of the valves of the shell are a sufficient indication that *Estheria* is a form which is well adapted for motion on firm ground, just as moreover, as a matter of fact, this animal

* A. Dohrn, "Geschichte des Krebstammes," Jenaische Zeitschrift für Medicin und Naturwissenschaften, Bd. vi., 1871, p. 149.

readily burrows in mud. In this respect among the three typical Euphyllopods it differs most widely from *Branchipus*, which appears to be the best swimmer of the group. *Apus* occupies about the middle position; it is a good swimmer, but is also fond of remaining at the bottom, where it digs up the mud with its shield *.

The Cladocera.

On considering the structure of the Cladocera we shall be struck by their great agreement with *Estheria*, while a comparison with *Apus* or *Branchipus* cannot be sustained in the same manner. A full idea of the far-reaching similarity between the two first-mentioned forms is acquired, however, when we select for comparison a young *Estheria* at a stage in which some six thoracic feet are present. A stage such as this was described by Joly †, by Ficker ‡, and likewise by Claus §, while by the latter it was also employed for the purpose of a searching comparison with the Cladocera, in the sense of the closest original relationship. An appeal to the existing statements on the subject will here suffice, and I will merely refer to the most important points of agreement.

In the Cladocera, just as in the case of *Estheria*, the body is laterally compressed. The shell is bivalve and covers the entire body, with the exception, however, of the head, which remains uncovered. The furcal end of the abdomen exhibits the development which is found only in the *Estheria*-type among the Euphyllopoda; as in the case of *Estheria*, it is bent towards the ventral surface and is furnished at its extremity with backwardly-directed hooks. The development of the second antenna as a swimming-organ is common to both the Cladocera and *Estheria*. Similarly the absence of the mandibular palp as well as the reduction of the two pairs of maxillæ, of which the second is entirely wanting in the Cladocera, has been inherited from the Euphyllopoda, in this case from *Estheria*. The shape of the thoracic feet can likewise be derived from that of those of *Estheria*, and the more

* For the statements as to these biological conditions I am indebted to Prof. Brauer. *Cf.* also Bronn's "Classen und Ordnungen des Thierreiches," *Arthropoda*, bearbeitet von A. Gerstaecker. I. *Crustacea*. Erste Hälfte, pp. 1049 *et seq.*

† N. Joly, "Recherches zoologiques, anatomiques et physiologiques sur l'*Isaura cycladoïdes*," Ann. Sc. Nat. 2e sér. t. xvii., 1842, p. 325.

‡ G. Ficker, "Zur Kenntniss der Entwicklung von *Estheria ticinensis*," Sitzungsber. k. Akad. Wiss. Wien, math.-naturw. Classe, Bd. 74, 1876.

§ C. Claus, 'Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceensystems,' Wien, 1876, p. 101.

elongated form of the foliaceous foot is rediscoverable among the Cladocera in genera such as *Sida*, which in all characteristics prove to be the most primitive. Lastly, mention must be made of the compound eyes, which, as in *Estheria*, meet together in the median plane to form a double eye, and, as in the genus referred to, are surrounded by a reduplicature of the skin, with the slight difference that the chamber which is formed above the eye by the overgrowth is in the case of the Cladocera completely closed *.

Claus has also suggested the two possibilities that the Cladocera are to be derived from larval forms of the Estheridæ or from a common ancestor with the latter, without, however, pursuing this question further. The passage referred to in Claus runs as follows:—"For my part there is no question of the fact that they [namely the Cladocera] are to be brought into closer relationship with the larval forms of the Estheridæ, and are to be derived, if not from these, at any rate from a common older ancestral form."

In my opinion this question may be answered with some degree of certainty by the theory that the Cladocera are to be derived from young stages of the Estheridæ.

The reasons to be adduced in favour of this are the following. In the first place the small number of body-segments in the Cladocera, a character which cannot be regarded as a primitive one, since extensive segmentation of the body must be assumed to have existed in old forms of Annulosa, and in the present case is easily to be proved by the fact that the forms *Branchipus* and *Apus* allied to *Estheria*, which is so close to the Cladocera, exhibit the same peculiarity †. Con-

* Grobben, *loc. cit.*

† There is probably no need to make especial mention of the fact that the number of the body-segments in the Euphyllopods is usually not so great as to necessitate our thinking of a *secondary multiplication of the body-segments*, of which instances are indeed found in the animal kingdom. The large number of appendages in the case of *Apus* is, in my opinion, to be explained by the theory that the appendages themselves have multiplied within the limits of the segment. But should the number of the appendages of this form actually correspond with the number of the body-segments which have coalesced to form a few larger annuli, the large number of body-segments which in this case we should have to recognize in *Apus* would have to be regarded as having been secondarily augmented. I would add merely incidentally that I cannot accept the multiplication of the ventral ganglia in *Apus*, which keeps pace with the increase in the number of the legs, as a proof that the body-rings of *Apus* are to be regarded as complexes of metameres.

But also supposing that the body-rings of *Apus* determine the number of the metameres, with regard to the increase in this number in many species of *Apus* (*e. g.* to about 45 in *Apus Lucasanus*, Pack.), a secondary multiplication of the body-segments would have to be taken into consideration, at least in the case of the more richly segmented species.

sequently the abundant segmentation of the body of *Estheria* appears to be a primitive condition, and likewise the diminished number of body-segments in the other Estheridæ, *Limnadia* and *Limnetis*, when viewed from this standpoint, is seen to be of a secondary nature. If therefore the Estheridæ distinguished by a smaller number of body-segments (*Limnadia* and *Limnetis*), and the Cladocera are to be derived from more richly segmented forms, the process must be imagined to have taken place in such a way that developmental stages of *Estheria* with a smaller number of segments constituted the starting-point for the other Estheridæ, which are composed of fewer segments, and likewise for the Cladocera.

A further argument in favour of the theory that the relatively unwieldy *Estheria* was the ancestor of the Cladocera is furnished by the peculiar shape of the end of the furca, which is adapted for motion on the bottom. If we consider the mode of life of the Cladocera we must designate it as pelagic. The Cladocera move about in the water with a hopping motion. It is true that there are also forms which live in the mud, like certain Linceids (*Monospilus*), but these are not representatives of primitive Cladocera. As such must be regarded the Sididæ, which live in clear water. Now, since the furca of the Cladoceran body points, by reason of its shape, to a mode of life upon the bottom, such as we actually see in the case of *Estheria*, the occurrence of such a furca in the case of the Cladocera is intelligible only if we derive them from forms living upon the bottom. Such a mode of life is, however, usually combined with a larger and heavier body; from this there results a further reason for deriving the Cladocera from an ancestral form distinguished by such characteristics, and for regarding them as Crustacea of the *Estheria*-type which have become adapted to the pelagic mode of life, in consequence of which their development has been arrested at a certain point.

A third piece of evidence in support of the view that the Cladocera are to be derived from a young form of *Estheria* is furnished by the condition of the compound eyes. In the Cladocera also the two compound eyes are united into an eye-bulb and overgrown by a reduplicature of the skin. As has already been shown in connexion with the discussion of the peculiarities of the *Estheria*-type, the forcing asunder and fusion of the two lateral eyes in *Estheria* is connected with the strong lateral compression of the head, and this again with the roofing-over of the head by the shell, and as being due to the same cause is also to be explained the overgrowth of the

double eye by a reduplicature of the skin. Now when, in the case of the Cladocera, in the development of the compound eye we find conditions which can only be understood on the theory of an original roofing-over of the head by the shell, these conditions appear as a character which has become established by inheritance, and belonged to an ancestral form whose shell enclosed the head at the sides, and was consequently developed in a similar manner to that which we find in the Estheridæ.

From all the reasons which have been adduced I can only decide in favour of the view that **young forms of Estheridæ, in** which the head was still unobscured by the shell, **were the ancestors from which the Cladocera were developed**; the peculiarities of the Cladocera which were previously mentioned are best understood on this assumption. A possible objection must, however, be considered; for if the overgrowth and fusion of the compound eyes already makes its appearance in *Estheria*-larvæ, in which the head still projects freely from the shell, this fact can only be regarded as a disturbance of the sequence of events in the ontogeny, but not as a proof of the view that the fusion and overgrowth of the eyes have arisen independently of the encasement of the head by the shell. But just as little can it serve as an argument against the theory which I have represented above, that the fusion and overgrowth of the eyes have arisen in the phylogeny only in consequence of the covering of the head by the shell, and therefore after and not before this.

Finally, I will quote the view expressed by Balfour* as to the origin of the Cladocera, according to which "the Cladocera have arisen from some Phyllopod form resembling *Estheria* by a process of regressive metamorphosis."

Since the Cladocera possess such an extensive structural agreement with the Estheridæ, that is, in the first instance, with the young stages of the latter, they are to be regarded as a very young branch of the Crustacea which have only lately split off from Estheridæ, such as we see them represented at the present time, and have become adapted to the pelagic mode of life. Lastly, I derive a similar conception on the part of Claus† from the genealogical tree of the Entomostraca which this investigator has set up, in which no special branch is shown for the Cladocera, which are supposed to be included in the Phyllopod group.

* F. M. Balfour, 'A Treatise on Comparative Embryology,' German edition, i. Bd., 1880, p. 438.

† C. Claus, "Neue Beiträge zur Morphologie der Crustaceen," Arbeiten des Zool. Institutes zu Wien, Bd. vi., 1885, p. 105.

The Ostracoda.

If the derivation of the Cladocera from *Estheria* succeeds without any difficulty, the same cannot be said of the derivation of the Ostracoda. Yet even in this case it is possible to obtain a sufficient number of connecting-links, such as may support the derivation of the Ostracoda from an Archiphyllopod form belonging to the *Estheria*-type.

In considering this question our attention must again in the first instance be directed to those forms of Ostracoda which appear to be the most primitive. These are to be found in *Cypridina*.

The first feature of the Ostracod body which strikes us is the complete enclosure of the laterally-compressed trunk by a large bivalve shell, which is closed by a muscle. On making an examination of the Euphyllopods, we find the same development of shell and the lateral compression of the body among the Estheridæ. The number of the body-segments is very small in the Ostracoda, and from reasons which have already been discussed this must be regarded as an instance of reduction from the number which were present in a more richly segmented ancestral form. The development of the posterior end of the body as a ventrally flexed furca, provided with hooks directed backwards, shows the entire agreement with the Estheridæ.

Among the appendages the first antenna appears to have a sensory character; yet in shape it is always similar to the appendages which subserve locomotion, and is similarly employed—a condition which, with reference to the original significance of the first antenna as a sense-organ, must be regarded as of a secondary character. The second antenna exhibits in *Cypridina* and likewise in *Halocypris* in a modified degree the form of the biramous swimming-foot-antenna as it persists among the Euphyllopoda in the adult condition in the Estheridæ alone, and appears as the most important organ devoted to the movement of swimming.

A great difference from the Estheridæ as well as from all the other Euphyllopods is seen in the shape of the mandibles and in the appendages of the Ostracoda which correspond to the two maxillæ of the Euphyllopods. The mandible is always provided with a foot-shaped palp, while this is wanting in all Euphyllopods at the period of the complete development of the body. As regards the appendages which are the homologues of the two maxillæ of the Euphyllopods, in the Ostracoda only the first of these is developed as a

maxilla; but, as opposed to the reduced maxilla of the Euphyllopods, it is seen to be still traceable to the original shape of the Phyllopod limb. The appendage which is the homologue of the second maxilla of the Euphyllopods is in the Ostracoda "still indeed armed with a maxillary process, yet chiefly constituted for locomotion as a foot" *, and therefore exhibits a general structural agreement with the following appendages. The oral appendages of the Ostracoda consequently undoubtedly display a more primitive shape than those of the existing Euphyllopods, in which degeneration of the mandibular palp and reduction of both maxillæ is a characteristic feature.

Of the characters to be employed for the purpose of comparison I will here further adduce only the compound eye of the Cypridinidæ, which has persisted exclusively in this Ostracod family. The compound eyes of *Cypridina* retain their original position at the sides of the head and have short stalks. Thus there takes place no fusion nor any overgrowth of the two eyes by a reduplicature of the skin, as is the case in the Estheridæ.

A renewed survey of the peculiarities of the Cypridinidæ reveals, on the one hand, characters which allow the Ostracoda to be brought into relation with the *Estheria*-type, thus —the bivalve character and the extent of the shell, which encloses the entire body, the ventrally flexed form of the furca, and the swimming-foot-antenna. On the other hand, however, the Ostracoda exhibit much more primitive characters in the short-stalked compound eyes of the Cypridinidæ, as well as in the development of the mandibles and of the appendages which are the homologues of the Euphyllopod maxillæ.

In answering the question as to how the peculiarities of the Ostracoda admit of being reconciled with the origin of the latter from Estheridæ, it is seen to be impossible to suppose that the Ostracoda are to be derived, like the Cladocera, from Estheridæ with the characters which they at present possess. On the contrary, it may be assumed with good reason that the Ostracoda sprang from old forms of Estheridæ which still possessed stalked eyes like *Branchipus*, and in which neither the reduction of the mandibular palp nor that of the two pairs of maxillæ had appeared, but in which the latter had the original foot-like shape. The peculiarities of the existing Estheridæ in these respects were only developed by them after the Ostracoda had branched off.

* *Cf.* C. Claus, 'Die Halocypriden des atlantischen Oceans und Mittelmeeres,' Wien, 1891, p. 28.

The idea that the lateral shoot formed by the Ostracoda branched off deep down from the Phyllopod stem also finds expression in the genealogical tree of the Entomostraca which Claus has set up *. The close affinity between the Ostracoda and the shell-bearing Phyllopods in particular has likewise been frequently alluded to, as, for instance, by Dohrn † and Claus ‡, as well as by Korschelt and Heider §.

The question as to whether the ancestral forms of the Ostracoda possessed a body composed of numerous segments is to be answered in the affirmative from the standpoint which has already been advanced, that an extensive segmentation of the body is to be assumed also for the old forms of Phyllopods, as being a phylogenetically older condition. In the Ostracoda we have to deal with a group of Crustacea which has proceeded from richly segmented ancient Phyllopods, of the habitus of the Estheridæ, by the process of loss of segments of the body.

The Copepoda.

There is no other section of Crustacea in which the entire development of the body has undergone such manifold modifications in accordance with the different mode of life as in the case of the present group. To enter into all these modifications not only lies outside the task which we have imposed upon ourselves, but also would in no way contribute towards answering the question which has been propounded. Here, as before, only those Copepoda which prove to be phylogenetically the oldest forms need be considered, and these are the Branchiura (*Argulus*), and among the Eucopepoda the Calanidæ (among which *Cetochilus* possesses the most primitive characters).

In respect of morphology the Branchiura are an extremely interesting group. The forms at present existing, which are represented only by two genera and few species, are parasitic as regards their nutrition, but have nevertheless retained the faculty of free locomotion. To the last-mentioned circumstance is probably also to be ascribed the retention of old characters.

That the Branchiura are to be assigned to the Copepoda,

* Claus, 'Neue Beiträge zur Morphologie der Crustaceen,' p. 105.

† Dohrn, 'Geschichte des Krebstammes,' pp. 133 and 149.

‡ Claus, 'Untersuchung zur Erforschung der genealogischen Grundlage des Crustaceensystems,' p. 97.

§ E. Korschelt and K. Heider, 'Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere.' Specieller Theil. ii. Heft, Jena, 1891, p. 500.

and among these represent a special group which contrasts with all others, was first demonstrated in a convincing fashion by Claus *. Above all the transformation of the oral appendage which is the homologue of the second maxilla into a double pair of maxillipeds, as is characteristic of the Copepoda, and then also the shape of the feet in the larval stage, may here suffice as important arguments.

But we also observe in the Branchiura manifold Phyllopod characters, which have always forced themselves upon the notice of investigators. Nevertheless, as for me, my first concern in this question is to inquire whether the Branchiura admit of comparison with existing Euphyllopods, and, if so, with which of them. That it is the **Apodidæ**, and these alone, that offer themselves for a closer comparison will appear from what follows.

The first resemblance between Argulidæ and Apodidæ which strikes us is seen in the shield-shaped development of the cephalothoracic carapace, which, in the case of *Argulus*, covers the three anterior segments of the thorax. This shield is continued as in *Apus* into the anterior margin of the head. Especially when we select for comparison the formation of the cephalothoracic shield in the larvæ of *Apus* the extensive agreement forces itself still further upon us. Claus was also struck by this resemblance, and with reference to it we find in his previously-quoted paper upon *Argulus*, in connexion with the comparison of the Argulidæ with the Siphonostomata, the following passage †:—"Should we wish to bring forward Phyllopods, in order to derive the Argulid form from them, we should be confined to the shield-shaped larvæ of *Apus*, whose mouth-parts are devoid of the maxilliped structures which are so characteristic of the Copepoda, and in conjunction with the foot-rudiments already bear the character of the Phyllopods. Nevertheless this comparison would in itself be morphologically apt, since in the shield-shaped dermal expansions of the parasitic Copepoda and of the young Phyllopoda we recognize equivalent structures." It is precisely upon the great resemblance in formation between the cephalothoracic shield and that of *Apus* that I would here primarily insist.

But there is yet a further peculiarity to be mentioned which *Argulus* has in common with *Apus*, and that is the possession of the compound lateral eyes, which, as in the case of *Apus*, appear to be sunken and covered by the skin. After finding

* C. Claus, "Ueber die Entwicklung, Organisation, und systematische Stellung der Arguliden," Zeitschr. f. wiss. Zool. Bd. 25, 1875.

† Claus, *loc. cit.* pp. 4, 5.

that the Phyllopod eye is overgrown by a reduplicature of the skin, I interpreted the capsule of the eye of *Argulus*, which was observed by Jurine * and Claus, as being of similar origin †. Subsequent investigations of mine, conducted it is true upon insufficient material, have, however, suggested to me the possibility that in the case of *Argulus* we may have to deal with a modification of the condition which is found in Estheridæ, Cladocera, and *Apus*. According to the figures which lie before me it would be possible that the eye simply separates from the integument and descends into the subjacent tissue. Nevertheless this does not exclude us from bringing both modes of formation into relation one with another and regarding them as modifications of essentially one and the same process. I consider the sinking-in and roofing-over of the compound lateral eyes of *Argulus* as an heirloom from the Apodidæ.

It is also possible to institute a comparison between the shape of the thoracic feet of *Argulus* and the special development exhibited by the foot of *Apus*. In *Argulus* the four pairs of thoracic feet are natatory appendages, and they each consist of a two-jointed axial portion and two narrow rami with many joint-like divisions, so that the entire limb reminds us of that of the Cirripedes. When brought into comparison with the swimming-feet of the existing Euphyllopods the foot of *Argulus*—and the larval conditions must not be left out of consideration—with its elongated stem and the likewise elongated slender rami, proves to resemble most the limb of *Apus* in shape. Herein I have in my mind the common general character of the two forms of limbs rather than an agreement which goes into details. With reference to the other points of agreement, that last alluded to appears to me to be no mere casual one, but to be based upon the close affinity between the two forms. Whether the flagellum which occurs on both the anterior pairs of feet in *Argulus* does not correspond to an epipodial appendage, and consequently is likewise to be regarded as an heirloom from ancestors resembling the Euphyllopods, I would not here attempt to decide; Claus compares it with the lancet-shaped branchial appendage of the Cirripede limb.

No connecting-points for phylogenetic investigations can be gained from the formation of the mouth-parts of *Argulus*, since in consequence of the parasitic mode of nutrition these appendages have been greatly modified. On the other hand,

* L. Jurine, "Mémoire sur l'*Argule foliacé*," Ann. de Mus. d'hist. nat. t. vii., 1806.

† Grobben, 'Die Entwicklungsgeschichte der *Moina rectirostris*,' p. 56.

the nervous system and digestive organs once more show resemblances to the conditions among the Euphyllopods.

In the organization of *Argulus* we consequently find peculiarities which remind us of *Apus* among the Phyllopods, while we also meet with Copepod characters, and, lastly, points of resemblance to the Cirripedes. For our present consideration the *Apus*-characters are of the first importance; we shall have to revert to the others again later on.

On submitting the characters of the Eucopepoda to examination with reference to the question under discussion, we meet with great difficulties at the first glance.

The segmentation of the body in the Eucopepoda is more extensive than in *Argulus*. While all segments are fully developed, as is seen also in the Calanidæ, the most primitive of Eucopepods, we find that in addition to the head five thoracic and five abdominal segments are present. In this respect, in comparison with the Branchiura, the Eucopepods exhibit a more primitive condition.

On the other hand, the cephalothoracic shield, which in *Argulus* is of fairly large proportions, is only extremely feebly developed in the Eucopepoda, and has undergone degeneration, no doubt in connexion with the rapid locomotion of these pelagic animals, for which a large carapace would be in no case of advantage. If we compare it with the shell-structures of the Euphyllopods we soon come to the conclusion that the cephalothoracic shield of the Eucopepods can only be referred to the shield of *Apus*. As in the case of *Apus* and also in *Argulus*, the edge of the rudimentary lateral reduplicature forming the cephalothoracic shield of the Eucopepods is continued into the anterior margin of the head. In general this condition appears more distinctly in the Nauplius-larvæ of the Eucopepoda, which also in other respects exhibit Euphyllopod characters, since moreover the shield of the Nauplius sometimes still possesses a broad flat shape. The flat development and the mode of connexion of the cephalothoracic shield with the anterior margin of the head already referred to belong to the *Apus*-character.

In the formation of the cephalic appendages the Eucopepoda exhibit more primitive conditions than the Branchiura. Here again it is the Calanidæ which will have to be considered. The first antenna in the Calanidæ, as in all free-living Copepods, is very long and serves for locomotion. Its colossal size in comparison with its original development as a sensory antenna and its utilization as an organ of locomotion are, like the analogous development of the first antenna among the Ostracoda, to be considered as of a secondary nature.

The second antenna has preserved the form of the biramous swimming-foot, while this is likewise retained in the palp of the mandible. The maxillæ and the double pair of maxillipeds, produced by the separation of the outer and inner rami of the second maxilla, exhibit the shape of the Phyllopod limb. As opposed to *Apus* the most primitive Eucopepods, the Calanidæ, with reference to what must be assumed to have been the ancestral forms of all existing Crustacea, possess more primitive characters in the retention of the biramous second antenna and of the mandibular foot, as well as of the foliaceous foot-shape of maxillæ and maxillipeds. In *Apus*, indeed, the second antenna is wanting in the adult state or is only present in a vestigial condition, and similarly the mandibular palpi are absent and both maxillæ reduced in size.

The thoracic feet of the Eucopepods exhibit the swimming-foot shape which is characteristic of the group—a two-jointed stem and a pair of three-jointed elongated rami. For their special shape a connexion is to be found in the case of *Apus* among the Euphyllopods. The special swimming-foot-like development of the limbs of *Apus* may here be emphasized once more. The Copepod foot, however, has lost the epipodial appendages by degeneration; the segmentation of its two rami was probably originally more extensive, as we may conclude from the shape of the foot in *Argulus*. The elongated form of the Eucopepod furca, too, occurs again among the Apodidæ, and in this connexion the larval conditions of the latter must in the first place be considered.

The compound lateral eyes have usually disappeared in adult Eucopepods, and are retained in a modified form only in the Pontellidæ*. On the other hand, I was able to prove† that in the Nauplius-stages of *Cetochilus* (and this in all probability also applies at least to the other free-living Eucopepods) extensive rudiments are present for the paired lateral eye, but these nevertheless undergo degeneration after they have severed their original connexion with the integument. Consequently, after the facts which have been adduced there can be no doubt that the ancestors of the Eucopepods possessed compound lateral eyes, and that these merely underwent degeneration at a later date. A comparison between the sinking-in of the eye of *Apus* and the severance of the eye-rudiments from the integument in *Cetochilus* as a

* *Cf.* C. Claus, "Das Medianauge der Crustaceen," Arbeit der zoolog. Instituts zu Wien, Bd. 9, 1891, p. 26.

† C. Grobben, "Die Entwicklungsgeschichte von *Cetochilus septentrionalis*," ibid. Bd. 3, 1881, pp. 20 and 36.

modification of the process must not be rejected, especially with reference to the position of the compound eyes in the larvæ of Cirripedes.

From what has been stated as to the Copepods the following conclusions may be drawn with regard to their affinity to the Euphyllopods :—Among the Copepods the Branchiura are in the first place to be considered as the group which in general have preserved what are phylogenetically more ancient characters, although in many respects, as in the formation of the cephalic appendages, secondary modifications have set in owing to the parasitic mode of nutrition. The Branchiura consequently represent a remnant of a primitive Archicopepod group. The isolated position occupied by the Branchiura among the Copepoda, as well as the small number of genera (*Argulus* and *Gyropeltis*) and species by which these animals are represented at the present day, are in accordance with this conception. In this sense, too, in the genealogical tree of the Entomostraca, to which reference has already several times been made, Claus has made the root of the Branchiuran twig arise from the bottom of the Copepod branch.

This Archicopepod group had, judging from the structure of *Argulus*, **the habitus of** *Apus*; consequently, according to my theory it is to be derived from that Archiphyllopod series which led to the existing Apodidæ, the character of which it already bore. Its branching-off from the *Apus*-series, however, took place at a period when the forms belonging to this series possessed the biramous swimming-foot-antenna, the mandibular foot, and foliaceous-foot-shaped maxillæ, and accordingly lies deep down on the stem of the Apodiform Archiphyllopods. To judge from the peculiarities of the lateral eye in *Argulus*, the sinking-in and covering-over of the compound lateral eyes were processes which already occurred in these ancestors of *Apus* from which the Copepods sprang. There is also no need to point out specially that the Copepods too, like the Ostracods, have proceeded from a much more extensively segmented form through reduction of the segments of the body.

The Cirripedia.

A consideration of the adult Cirripedes furnishes but very few points of importance for the answering of the question as to their origin. This is moreover to be accounted for by the altogether exceptional mode of the attachment of these animals by the cephalic end, and the changes in the develop-

ment of many organs which ensue from these conditions. In the case of the Cirripedes it is chiefly the developmental stages that furnish the evidence necessary for the question of origin.

Among the Cirripedes the Lepadidæ (forms like *Pollicipes**) are to be regarded as the most primitive. The first thing which strikes us in the organization of this family, besides the peduncle-shaped development of the cephalic end, is the complete enclosure of the body by a mantle-shaped shell. The mouth-parts are short, the mandibles devoid of palps, the two pairs of maxillæ small. Of the two antennæ the second has disappeared, while the first serves as an organ of attachment. The six pairs of thoracic legs are provided with long many-jointed rami thickly clothed with setæ, and the abdomen appears to be completely reduced.

Above all, the mantle-shaped shell reminds us of the bivalve shell of the Estheridæ, and would afford justification for a derivation from Archiphyllopods resembling *Estheria*. Yet a closer consideration of the developmental stages shows that such a derivation is incapable of accomplishment, since these stages structurally conform to the conditions found in the Copepods and in the Apodidæ among the Euphyllopods.

The extensive structural agreement between the developmental stages of the Cirripedes and those of the Copepods was demonstrated by Pagenstecher † and Claus ‡. The Cirripede Nauplius closely resembles the Copepod Nauplius, and in the so-called *Cypris* stage the shape of the thoracic feet as swimming-appendages, as well as the segmentation of the abdomen and the formation of the furca, repeat the conditions which exist in the case of the Copepods.

Since the idea that the Cirripedes are closely allied to the Copepods appears to be thoroughly in accordance with facts, it must also be possible to derive the Cirripedes, like the Copepods, from Archiphyllopods which possessed the habitus of *Apus*. As a matter of fact, such points of agreement with

* *Cf.* A. Weithofer, "Bemerkungen über eine fossile *Scalpellum*-Art aus dem Schlier von Ottnang und Kremsmünster, sowie über Cirripedien im Allgemeinen," Jahrbuch der k. k. geolog. Reichsanstalt, 1887, 37 Bd., p. 376.

† A. Pagenstecher, "Untersuchungen über niedere Seethiere aus Cette.—IX. Beitrag zur Anatomie und Entwicklungsgeschichte von *Lepas pectinata*," Zeitschr. f. wiss. Zool. Bd. 13, 1863.

‡ C. Claus, "Die Cypris-ähnliche Larve (Puppe) der Cirripedien und ihre Verwandlung in das festsitzende Thier," Schriften der Gesellsch. zur Beförderung der gesammten Naturwiss. zu Marburg, Supplementheft v., 1869. Also 'Untersuchungen zur Erforschung der genealog. Grundlage des Crustaceensystems,' pp. 79–88.

Apus can be shown to exist, and they are to be looked for in the first instance in the Nauplius conditions. The Nauplius of the Cirripedes agrees with that of the Phyllopods, and among these with that of *Apus*, even more than with the Copepod Nauplius. As *Apus*-like characters I may point out the shield-shaped expansion of the shell, which is directly continuous with the anterior margin of the head, and moreover the presence of the compound lateral eyes, which, as in the case of *Apus*, lie beneath the integument. The lateral eyes have separated from the skin and are deep-seated, and consequently in this respect they agree with the rudiments of the lateral eyes of the Eucopepod Nauplius (and probably also of *Argulus*). As in the latter case, so in that of the Cirripedes, I regard the separation of the eyes from the skin and their downward change of position as a modification of the process observed in *Apus*, where the eye is overgrown by the integument. In the so-called *Cypris* stage of the Cirripedes also the compound eye retains this position.

If the comparison just instituted is correct we must expect to find still more points of agreement with the Cirripedes in the case of the Argulidæ than in that of the Eucopepoda. This also is exactly what takes place. The paired lateral eyes of *Argulus*, which have likewise passed beneath the skin, are copies of the paired eyes of the Cirripede Nauplius. The thoracic feet of *Argulus* show a similarity to the Cirripede limbs, as has already been asserted by Claus, and also the flagellum of the two first thoracic feet of *Argulus* might, according to Claus *, be comparable to the lancet-shaped appendage of the Cirripedes, in which case, however, it might still correspond to an epipodite. *Argulus* consequently does not merely prove to be a form intermediate between the Apodidæ and Eucopepods, but also possesses the same significance between Cirripedes and Copepods. In *Argulus* therefore we find a mixture of characters belonging to Copepods, Cirripedes, and *Apus*.

Since, as I think, an objection can hardly be raised to the close affinity of the Cirripedes to the Copepods, we now arrive at a solution of the question as to how we are to interpret the bivalve shell of the Cirripedes. We must agree with Pagenstecher and Claus † in regarding the bivalve Cirripede shell as a special adaptation from the shield-shaped rudimentary shell as it appears in the Copepod Nauplius. It has conse-

* C. Claus, 'Ueber die Entwicklung, Organisation, &c. der Arguliden,' p. 34.

† C. Claus, 'Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceensystems,' p. 83.

quently proceeded from the flat shell. This being so, still less do we meet with any difficulty in deriving the formation of the shell of the Cirripedes from the shell of *Apus*.

The Cirripede shell is, however, only apparently bivalve, and its similarity to the Ostracod shell in the so-called *Cypris* stage is merely external. From the condition of the shell in this stage its agreement with the shell of *Apus* can still be demonstrated in spite of the external dissimilarity. A closer consideration of the shell in the *Cypris*-like larva shows that the shell is anteriorly **directly continuous with the anterior margin of the head.**

Thus it also comes to pass that the right and left portions of the shell are united on the ventral side in the anterior half of the animal, and the cleft which leads into the mantle-cavity only commences far back. The shell of the Cirripedes is consequently an undivided one, as in *Apus*, merely extending backwards in direct continuation of the anterior margin of the head. It would therefore be advisable not to call the Cirripede shell bivalve, but to exclusively apply to it the often-used term " mantle-shaped " (" mantelförmig ").

With reference to the common origin of Copepods and Cirripedes, which results from the foregoing, it only remains to discuss the mouth-parts of the latter, on account of their different formation from those of the Copepods. The shape of the mouth-parts of the Eucopepods, such as *Cetochilus*, which have to be cited in this comparison, exhibits primitive conditions, as has already been shown. In the Cirripedes, on the other hand, the mandibles are devoid of palps, while the two pairs of maxillæ which follow them appear reduced and developed in such a way that the similarity of the mouth-organs to those of the Euphyllopods is certainly great. From this circumstance a decided difficulty would result as regards a common derivation for the Copepods and Cirripedes, and it would be an argument in favour of a separate origin of the Cirripedes from the Archiphyllopods if this similarity of the mouth-parts were to be explained as being due to direct inheritance; in addition to this there would be the fact that, while for the Archiphyllopod ancestral form of the Copepods the possession of palp-bearing mandibles and maxillæ in the shape of foliaceous feet is to be presupposed, the Cirripedes would have to be derived from forms in which the formation of the mouth-parts which is characteristic for all existing Euphyllopods must already have appeared. Taking into consideration the great agreement between the Cirripedes and Copepods in, as it seems to me, more important characters, the similarity in development between the mouth-organs of

the Cirripedes and those of the Euphyllopods is to be interpreted as an adaptation which has been evolved independently in this lateral branch from foot-like mouth-organs.

The Cirripedes therefore in all probability are of common origin with the Copepods and sprang from Archiphyllopods, as is also represented by Claus in his genealogical tree of the Entomostraca, and, moreover, they arose deep down from forms which as yet showed no reduction of the mouth-parts. **This Archiphyllopod ancestral form of the Copepods and Cirripedes belonged—and to this I would here attach especial weight—according to its habitus to the Apus-series.** The agreement to be detected in many respects between the Argulidæ and Cirripedes indicates that the root of the former is to be sought in the neighbourhood of the fork of the common branch for Copepods and Cirripedes.

The view that the Cirripedes and Copepods belong to a common stem has not been undisputed. Thus it has been represented by Balfour * that the Cirripedes are to be derived directly from an old form of Phyllopod with two shells. The development of the shell and also the possession of the paired lateral eyes, as well as the larval history of the Cirripedes, were the decisive points in Balfour's opinion. This author regards the so-called *Cypris*-stage in the development of Cirripedes as a phyletic one which "more or less accurately represents an ancestral form of the Cirripedes," and he considers that "both the bivalve shell as well as the compound eyes are ancestral characters." To the similarity in shape at this stage between the thoracic appendages and Copepod feet Balfour attaches no great weight.

Balfour is entirely correct in designating the compound lateral eyes as ancestral characters; but these constitute no difficulty in the way of a common origin of Copepods and Cirripedes, since the Argulidæ possess the paired eye, and rudiments of the lateral eyes are also formed in the Eucopepod Nauplius, but afterwards merely undergo degeneration. On the other hand, it has already been shown that a close comparison of the mantle-shaped Cirripede shell with the bivalve shell-formations is untenable, and that it appears possible to derive the shell of the Cirripedes from a shield-shaped one. From this it appears that the peculiar formation of the shell is a cœnogenetic character of the larvæ. And yet it is simply and solely this superficial agreement of the shell of the so-called *Cypris*-stage with that of the Ostracods

* F. M. Balfour, 'Comparative Embryology,' German translation, i. Bd., 1880, p. 482.

that occasions the similarity of this larval stage to the bivalve Crustacean forms, while the shape of the thoracic feet, of the abdomen, and of its furcal appendages completely exhibits the Copepod character, and there is nothing in the way of the interpretation of these features as being of phyletic value. The absence of the second antenna is explicable as being due to the mode of life of the Cirripedes, and to be understood from the modification of the entire animal in consequence of its having become fixed. In this connexion I would further remark that the loss of the second antenna in the Cirripede group has developed independently and is in no way to be brought into genetic relation with the loss of the same appendage in the existing Apodidæ.

The theories of Balfour are shared also by Fowler *, who, however, in opposition to Balfour imagines a common origin for the Cirripedes and Ostracods from Archiphyllopod forms, and consequently goes even further than Balfour, who supposes that the Ostracods originated independently from the main Crustacean stem.

In agreement with Balfour, Korschelt and Heider † also assume that the Cirripedes arose from an Archiphyllopod form provided with a bivalve shell and, indeed, resembling the ancestral form of the Ostracods. In forming their decision as to the ancestral form of the Cirripedes, Korschelt and Heider likewise base their conclusions upon the *Cypris*-like larva. They assign no decisive value to the resemblance in the formation of the thoracic appendages, nor to the agreement between this larval stage and the Copepods with reference to the number of the segments of the body, since these points could have been acquired independently. On the other hand, the presence of the large bivalve shell is considered to be of primary importance, while after this the absence of the typical Copepod characters (degeneration of the lateral eyes and of the dorsal shield, and cleavage of the second maxilla into a double pair of maxillipeds) in the so-called *Cypris*-larva of the Cirripedes is also alluded to.

With reference to the first-mentioned point I may appeal to what has already been stated, and I would merely add that I too, in forming a decision as to the common origin of the Copepods and Cirripedes, attach no special weight to the agreement in the number of the segments of the body in each

* G. H. Fowler, "A Remarkable Crustacean Parasite, and its Bearing on the Phylogeny of the Entomostraca," Quart. Journ. Micr. Sci. vol. xxx. 1890, pp. 115–119.

† Korschelt and Heider, "Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere.—Specieller Theil," ii. Heft, pp. 500–501.

case, although I regard the fact as worthy of notice, and I am inclined to consider this agreement as only of secondary importance.

With regard, however, to the absence of the above-mentioned typical Copepod characters in the case of the *Cypris*-like larva of the Cirripedes, it appears to me that we ought not to expect to find these characters at all in the larva in question. A common origin for Copepods and Cirripedes is not to be taken to mean that the Cirripedes sprang from typical Copepods (*i. e.* of the Eucopepod type), but that they arose from an ancestral form which was common to both groups, and in which those most typical Copepod characters were not yet developed. The ancestral form was consequently an animal in which, to refer to what are rightly indicated in this connexion by Korschelt and Heider as Copepod characters, the paired lateral eyes, as well as a broad dorsal shield, were still present, and the conversion of the second maxillæ into the double pair of maxillipeds had not yet set in, while the thoracic feet perhaps agreed in shape with those of *Argulus*.

On the same grounds is to be found the solution of the supposed difficulty raised by Hoek *, that the *Cypris*-like larva, which is so characteristic of the ontogeny of the Cirripedes, is altogether absent in the development of the Copepods. The *Cypris*-larva of the Cirripedes is a typical Cirripede stage, and was acquired by these Crustacea at a period when they had already separated from the ancestral form which was common to the Copepods as well as to themselves.

The Malacostraca.

The Malacostraca constitute a well-defined natural group. In the Leptostraca (*Nebalia*) there are preserved for us remnants of an old Crustacean type, which may with justice be regarded as being very closely allied to the ancestral form of the existing Malacostraca. On the other hand the Leptostraca exhibit peculiarities which remind us of the Euphyllopods.

As primitive characters of *Nebalia*, when contrasted with the other Malacostraca, we must regard the number of the abdominal segments, which is one in excess of that found in the remainder of the group, the preservation of the furca, the foliaceous shape of the thoracic appendages, which represent a mixture of the Schizopod and Phyllopod foot, and lastly in all probability also the shape of the shell.

* P. P. C. Hoek, "Report on the Cirripedia collected by H.M.S. 'Challenger' during the years 1873–76: Zoology, Part xxv.," 1883, p. 17.

The latter three peculiarities are to be regarded as Phyllopod characters, and with them in like manner must also be classed the stalked eye.

The attempt to bring *Nebalia* into closer comparison with one of the three Euphyllopod types proves to be more difficult than in the case of the other groups of Crustacea. In this instance the quickest way of arriving at a result will be by the process of exclusion.

A closer comparison between Estheridæ and *Nebalia*, which might appear to be justified on the basis of a certain similarity in the shell, is soon found to be impossible. In this connexion I merely recall the development of the postabdomen and furca which is characteristic of the Estheridæ, where this portion of the body appears ventrally flexed and terminates with claws. If the Apodidæ be adduced, the shield-shaped formation of the shell as well as the peculiar habit of the thoracic limbs again admit of no connexion. Consequently *Branchipus* alone remains, to which most resemblances may be pointed out. On the one hand we have the development of the branches of the caudal fork, which in *Nebalia* so greatly resemble those of *Branchipus*, owing to their form and the fact that they bear setæ along their entire margin, that the term "branchipodiform" has been applied to them by Claus*. As a further point of agreement we next come to the stalked condition of the eyes, as well as the shape of the thoracic limbs of *Nebalia*, which bears most analogy to the foliaceous form found in *Branchipus*, although in this respect the resemblance is much smaller. These, however, are the only characters which can be turned to account for the purpose of establishing a closer affinity between *Nebalia* and *Branchipus*.

In my opinion the difficulty of this comparison lies in the manifold modification which is exhibited by the *Branchipus* type when contrasted with its probable ancestors. The very absence of a shell gives *Branchipus* a greatly altered appearance as opposed to the other types; this condition is probably to be explained as being due to the loss of a shell which was originally present. This may perhaps have resembled the shell of *Nebalia* in shape; whether it also possessed the cephalic valve (Kopfklappe) can scarcely be determined. The sharp division, too, between thorax and abdomen in *Branchipus* proves to be a secondary condition. Since the number of the thoracic and abdominal segments does not agree with that of those of *Nebalia*, in which there is similarly a

* C. Claus, "Ueber den Organismus der Nebaliden und die systematische Stellung der Leptostraken": Arbeiten aus dem zoolog. Institut zu Wien, Bd. viii. 1888, p. 128.

sharp demarcation between thorax and abdomen, this separation of the two regions of the body cannot be utilized as a proof of a closer affinity between the two forms referred to. In the possession of appendages upon six of the abdominal segments *Nebalia* exhibits more primitive conditions than *Branchipus*, in which the abdomen is devoid of limbs. The special development of the second antenna, as well as of the oral appendages of *Branchipus*, and the agreement of the latter organs with those of the rest of the Euphyllopods would, since this is undoubtedly likewise a case of secondary transformations of appendages which were originally differently constituted, not have much weight in this comparison with *Nebalia*, where in these respects much more primitive conditions are to be met with.

While considering all the circumstances which have been indicated, we shall still find ourselves continually reverting to *Branchipus* in our search for a connexion with *Nebalia* among the existing Euphyllopods. The supposition that in the *Branchipus* type we may actually recognize an Archiphyllopod remnant, from which the Malacostraca have arisen, will, as containing much probability, find a further support in a subsequent consideration.

Into the relationships of the different groups of Malacostraca I need not enter further. A genealogical tree, which best exhibits the affinity of the Malacostraca, has been set up by Claus *, and the reader may be recommended to consult it. I would merely suggest that the origin of the lateral branch for the Stomatopoda as represented in it should be moved somewhat higher up, and indeed that it should not be sought for until the Archischizopods are reached, from which, in my opinion, the Stomatopoda have developed as a separate offshoot. Above all, the youngest Stomatopod larva (*Erichthoidina*), which was described by Claus †, exhibits such manifold relations to the Schizopods that the view which I have expressed appears to be thereby confirmed.

While on this subject I would nevertheless refer to a peculiarity of the Stomatopods, as opposed to all other Malacostraca with the exception of *Nebalia*, which has not hitherto been sufficiently appreciated. This is the *rostral plate*, which appears in various shapes, and is jointed to the anterior margin of the cephalo-thoracic shield. The structure in question reminds us of the cephalic valve of *Nebalia*, with which it is

* C. Claus, 'Neue Beiträge zur Morphologie der Crustaceen,' p. 104.

† C. Claus, "Die Metamorphose der Squilliden": Abhandlungen der königl. Gesellschaft der Wissenschaften zu Göttingen, xvi. Bd. 1871, Taf. i. fig 1.

probably also homologous. So far as can be concluded from the observations at present available *, it must be supposed to arise by being segmented off from the anterior margin of the cephalo-thoracic shield, just as also in the case of *Nebalia* the cephalic valve arises in this manner. The development of the rostral plate of the Stomatopods is connected with the segmenting off of the anterior part of the head, which bears the eyes and the first antennæ. I would at any rate regard it as an heirloom from *Nebalia*, which has been preserved with a peculiarity in the formation of the head, or else has developed again by a process of atavism. In the event of this interpretation being correct, we may draw from it the further conclusion that the rostral plate (cephalic valve), or at least a corresponding process, developed for the protection of the stalked eyes, probably also formed part of the primitive *Branchipus*-shell, and that this was no longer developed among the Schizopods, as well as the forms arising from them, but that the portion equivalent to it is to be looked for in the rostrum of the shell, which thereby acquires a heightened interest from a morphological point of view. The possession of a movable rostral plate is to be assumed for the Archischizopods. Finally, it must be further remarked that Claus † has expressed himself in opposition to a homologization of the cephalic valve of *Nebalia* with the rostrum of the Malacostracan shell ‡.

Summary and Conclusion.

In the preceding pages the attempt has been made to refer the Crustacea which are united in the group Entomostraca, as well as the Malacostraca, to the three types which are to be distinguished among the Euphyllopods existing at the present day, namely, *Branchipus*, *Apus*, and *Estheria*. On making a comparison between the most essential characters in the different outward structure of these forms it has been found that the Cladocera and Ostracoda can be referred to ancestral forms resembling *Estheria*, while the Copepoda and Cirripedia

* *Cf.* Claus, *loc. cit.* pp. 133 & 142.

† Claus, "Ueber den Organismus der Nebaliden, &c.," p. 39.

‡ I feel bound to remark that, on the other hand, I, in accordance with Claus (*loc. cit.*), do not regard as justifiable the homologization of the cephalic valve of *Nebalia* with the rostrum of the Copepods, to which G. O. Sars ("Report on the Phyllocarida collected by H.M.S. 'Challenger' during the years 1873-1876:" The Voyage of H.M.S. 'Challenger,' Zoology, vol. xix. 1887, p. 31) alludes. The so-called rostrum of the Copepods has nothing to do with that of the Malacostraca, and has arisen entirely independently in the Copepod group.

admit of being traced back to an ancestral form like *Apus*, and the Malacostraca probably to one of which a remnant is represented by the *Branchipus*-type.

That the three Euphyllopod types, which are so different in outward appearance, can be regarded as remnants of ancestral forms which presented a general agreement with them, is also conversely again rendered probable by the existence of Crustacean groups bearing characters of these types in the Animal Kingdom of to-day. **The existence of the three Euphyllopod types, *Branchipus*, *Apus*, and *Estheria*, and that of Crustacea which are referable to these types, are facts which mutually support one another.**

In order to prove this proposition, I must go somewhat further afield.

I believe I am correct in stating that Hatschek* was the first to declare that only when a larval or embryonic form of higher animals exhibits a great agreement with the adult stage of lower animals is it possible to conclude with much probability that this corresponds to a similar ancestral form. Thus, we should not be in a position to conclude with a similar show of probability that the Trochosphere larva of the Annelids and Mollusks is a repetition of an ancient ancestral form which resembled it, if there were not still in existence at the present day Rotifers exhibiting great agreement with the Trochosphere stage.

From the existence of developmental stages, which we recognize as of phyletic value, may be drawn the further conclusion that similar conditions in the form of sexually mature animals must not only have existed during a long period of time, but also must manifestly have enjoyed a wide distribution. The idea that a form of this kind was once widely distributed is again supported by the fact that animal types agreeing with such developmental stages in structure have persisted until the present time.

From the application of these propositions a further support may be gained for the views which have been developed by me with reference to the origin of the Crustacea.

If in the existing Animal Kingdom we find three Euphyllopod types which are strikingly different in appearance, and all other Crustaceans at present living show certain points of agreement with these three types, then, as it seems to me, additional probability has in consequence been gained, not only for the theory that these three Euphyllopod types represent remnants of Crustacea which were formerly very

* B. Hatschek, 'Lehrbuch der Zoologie,' Erste Lieferung, 1888, pp. 25, 26.

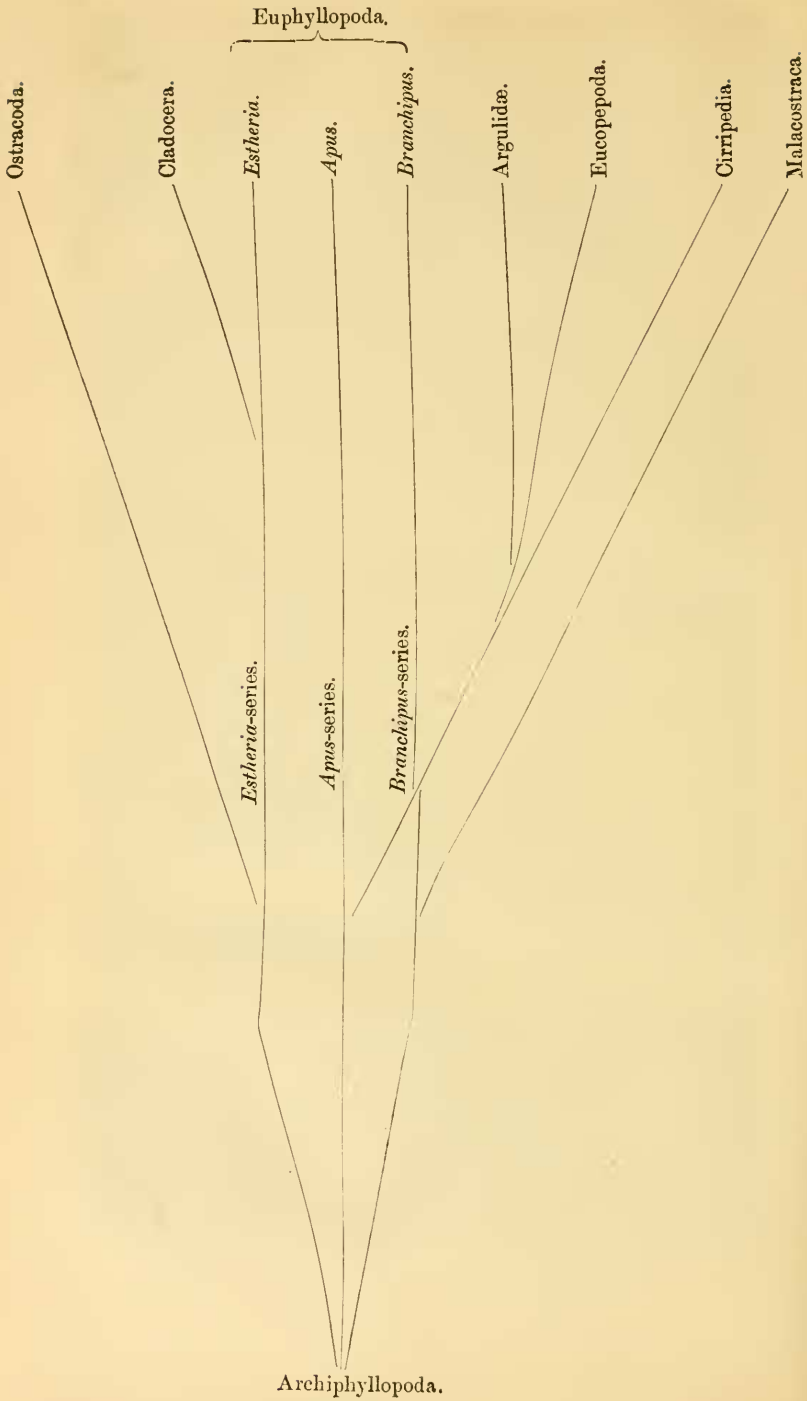
widely distributed, but also for the view that the rest of the Crustacea at present in existence are referable to the three types in question. In the special application of this conclusion to the *Branchipus*-type, I derive from the fact of the preservation of this type and of the high development of that of the Malacostraca a further proof of the theory that the special points of agreement, albeit only small, between the two types may be turned to account in the sense of establishing a closer affinity, and that consequently the Malacostraca are referable to the *Branchipus*-type.

So far as is possible I have endeavoured to establish the view cherished by myself, that the Ostracoda and Cladocera admit of being traced back to the *Estheria*-type of the Euphyllopoda, the Copepoda and Cirripedia to that of *Apus*, and the Malacostraca to that of *Branchipus*, and that the existing Crustacea are to be derived from three ancestral forms corresponding to these types. The following genealogy (p. 468), which, moreover, essentially agrees with that set up by Claus, repeats this conception in tabular form.

From this genealogical tree it is evident that the *Branchipus*-series in ancient times gave origin to a great Crustacean group, that of the Malacostraca; that to the *Apus*-series is likewise to be traced a great group, comprising the Copepoda and Cirripedia; and that, lastly, the *Estheria*-series in ancient times also gave rise to a similar stem, that of the Ostracoda, while at a more recent date it once more gave off a lateral branch in the shape of the Cladocera *. A further point in agreement with the theory that the Cladoceran stem did not arise until a later period is the existence of an intermediate series leading to the Cladocera and consisting of different genera of Estheridæ (*Limnadia*, *Limnetis*), while all other groups of Crustacea appear to be sharply separated from the Euphyllopods at present living.

According to these conceptions it is possible to establish a natural system of classification among the Crustacea of which the Entomostracan group is composed, from which there also

* This is probably the best place to quote the following statement by Dohrn ('Geschichte des Krebstammes,' p. 132), since we may gather from it that Dohrn asked himself the question how the existing Euphyllopod types are related to the other Crustacean groups in respect of phylogeny. The passage in question runs as follows:—"But however it may be with regard to Gigantostraca and Trilobites, in any case the order Phyllopoda remains the matrix for all other forms of Crustacea at present in existence. It is true that there is no way leading us into one of the other orders either through *Apus* or through *Branchipus*, but from *Nebalia* as well as from the shell-bearers we have to follow the course of the development of powerful series of forms."


Euphyllopoda.
Ostracoda.
Cladocera.
Estheria.
Apus.
Branchipus.
Argulidæ.
Eucopepoda.
Cirripedia.
Malacostraca.
Estheria-series.
Apus-series.
Branchipus-series.
Archiphyllopoda.

results an alteration in the classification of the Crustacea in general. **The group Entomostraca should be dissolved, and a number of groups formed from it, which are to be considered as equivalent to the Malacostraca.** One of these natural divisions is formed by the Euphyllopods in conjunction with the Cladocera; the Ostracoda are to be regarded as a second special group of equal value, which has arisen from the *Estheria*-type. The Copepoda and Cirripedia admit of being combined in a third group, which may be designated *Apodiformes*. In accordance with this the Ostracoda may be termed *Estheriæformes*—a group, however, into which the Cladocera cannot be received, on account of their separate origin from the *Estheria*-series; the Cladocera must remain united with the Euphyllopods, since they are derived from Estheridæ of the recent type. A fourth large natural group, which can be traced back to the *Branchipus*-series, is constituted by the Malacostraca. In conformity with the designations previously chosen, this group also might be named *Branchipodiformes*.

The classificatory system of the Crustacea would consequently assume the following shape :—

Class **CRUSTACEA.**

Subclass I. PHYLLOPODA.

Order 1. *Euphyllopoda.*
2. *Cladocera.*

Subclass II. ESTHERIÆFORMES.

Order *Ostracoda.*

Subclass III. APODIFORMES.

Order 1. *Copepoda.*
2. *Cirripedia.*

Subclass IV. MALACOSTRACA (Branchipodiformes).

I. Leptostraca.

Order *Nebaliadæ.*

II. Eumalacostraca.

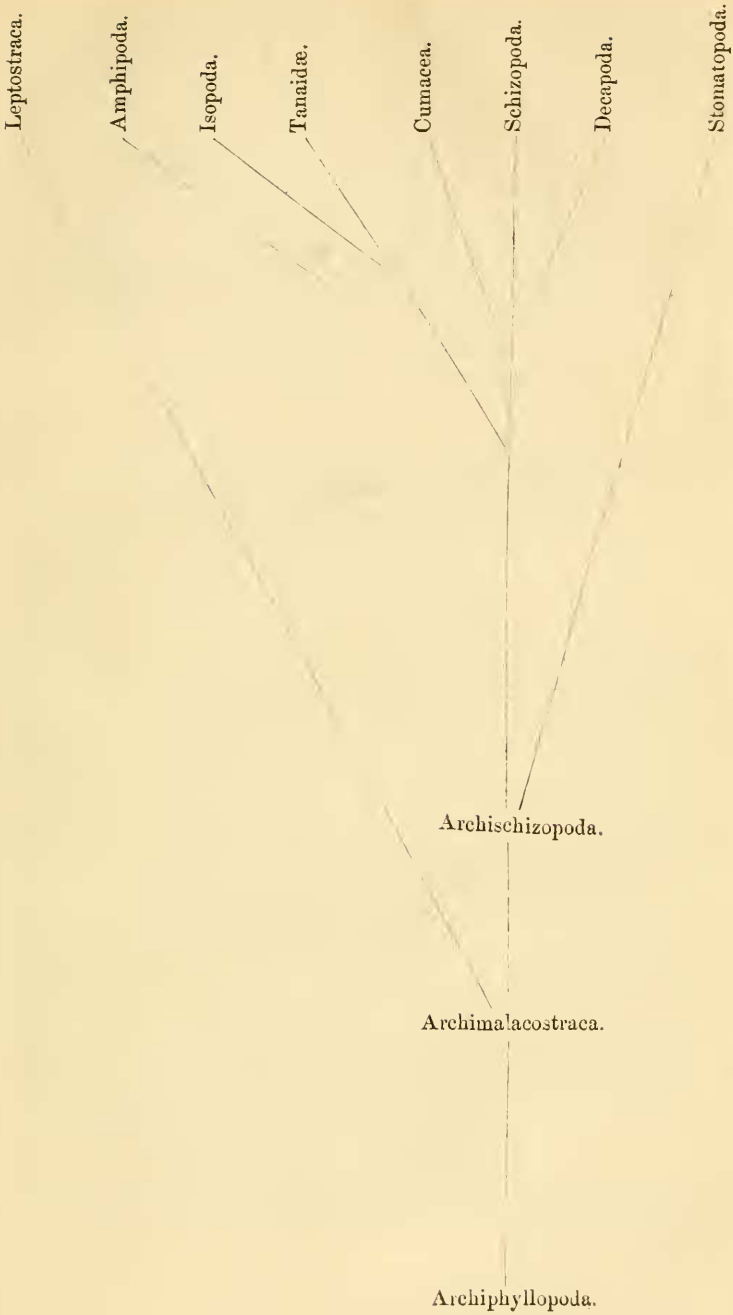
Order 1. *Stomatopoda.*
2. *Thoracostraca.*
3. *Arthrostraca.*

In a similar manner Balfour * has already divided the Crustacea into a number of groups and has distinguished the following sections as of equal value:—I. Branchiopoda; II. Malacostraca; III. Copepoda; IV. Cirripedia; V. Ostracoda. Although the guiding points of view of the descent appear similarly decisive in Balfour's case also for the foundation of these groups, they differ from mine in so far as a tracing-back of these groups to the three Phyllopod types is not considered.

With reference to the subdivision of the Malacostraca, I would remark that the Arthrostraca and Thoracostraca represent the groups distinguished by Claus, with the difference that I set them down as orders. The separation of the Stomatopoda as a special group equivalent to the Arthrostraca and Thoracostraca appears to me to be well-founded, owing to the great difference which these Crustaceans exhibit when contrasted with the other Thoracostraca with which they were united. It corresponds to the theory of their separate origin from Archischizopods, as I have already explained. Claus † interprets the great difference between the Stomatopoda and the rest of the Thoracostraca and Arthrostraca in somewhat different fashion, since he even regards the Stomatopoda as having arisen separately from Archimalacostraca. The agreement of the Stomatopoda with the Thoracostraca and Arthrostraca in the formation of the telson and in the number of the abdominal segments, as well as the great agreement of the youngest known *Erichthoidina*-larva with the Schizopods, decides me to combine the Stomatopods as Eumalacostraca with the two groups mentioned, and to derive them all from Archischizopods, and, on the other hand, to place the Leptostraca, which, with Claus, we must regard as remnants of Archimalacostraca, in contrast to the Eumalacostraca. By the retention of the branchipodiform furca, the larger number of the abdominal segments, and the peculiar shape of the thoracic feet as well as of the shell, the Leptostraca are proved to be much more primitive than all other Malacostraca. In order to give clear expression to my view as to the affinities of the Stomatopoda, the genealogical tree of the Malacostraca may here be given; its agreement in other respects with that set up by Claus will appear from a comparison of the two.

* Balfour, *op. cit.* p. 434, note 1.

† Claus, 'Neue Beiträge zur Morphologie der Crustaceen,' pp. 96 and 104.


Leptostraca.
Amphipoda.
Isopoda.
Tanaidæ.
Cumacea.
Schizopoda.
Decapoda.
Stomatopoda.
Archischizopoda.
Archimalacostraca.
Archiphyllopoda.

With reference to the Euphyllopods, there is, however, a difficulty still to be disposed of. If the views which I have here set down are correct, and in the existing Crustacea are to be seen the descendants of three Archiphyllopods which differed in outward form and may be met with again in the three types, *Branchipus*, *Apus*, and *Estheria*, what is the explanation of the fact that in these three representatives of old ancestral forms, which have at any rate existed side by side for a long time separated in three series of forms of different *habitus*, the degeneration of the mandibular palp and the reduction of both maxillæ is to be found in the same manner? That the peculiar development of the mouth-parts in existing Euphyllopods is a secondary character will not be questioned any more than the assumption that the old ancestral forms possessed mandibular palp and maxillæ like foliaceous feet, as is evident from the existence of such mouth-parts in the case of the Ostracoda, Copepoda, and Malacostraca.

In my opinion the degeneration of the mandibular palp, as well as the diminution in size of the maxillæ in the *Branchipus*-, *Apus*-, and *Estheria*-series of Euphyllopods, took place independently, and are to be explained as an instance of convergence. This convergence finds a further explanation in the origin of the three series alluded to from a common primitive form, in which there existed a similar tendency to development in the directions indicated. Moreover we find that the degeneration of the mandibular palp is of frequent occurrence, as in the Cyclopidæ among Copepods and also in the Cirripedia, which latter also possess maxillæ of a diminished size.

In so far as a proof can be given I have endeavoured to give it, in order to establish the view that the three Euphyllopod types at present existing, which are so very divergent from one another in external structure, are remnants of three ancient Archiphyllopod series to which the rest of the Crustacea now living can be traced back. The changes in the system of classification are merely the result of these views.

That much that was already known has been repeated in the course of the argument cannot be made a subject of reproach against this consideration of the question, since it is chiefly a case of fresh combination of known facts. Neither can blame be attached to the omission to notice many systems of organs, since many of these furnish no points for my argument. It is self-evident that only those organs could be brought forward in which sufficient differences in formation appear with reference to their resemblance to the three Euphyllopod types.

A retrospect of the speculations which have been set up and the views which have been expressed will allow much to appear as requiring to be confirmed by further observation. Nevertheless we should not under-estimate the difficulty of proof in the treatment of a question in which sometimes even but slight indications of old peculiarities must be of importance. This difficulty, however, will not be permitted to suppress the attempt at an elucidation. The circumstance that arguments may really be pointed out everywhere will allow this consideration of the case to appear admissible, while the fact that every attempt at an elucidation ought to be made will show that it is justifiable.

LXXIII.—*Report upon the Stomatopod Crustaceans obtained by P. W. Basset-Smith, Esq., Surgeon R.N., during the Cruise, in the Australian and China Seas, of H.M.S. 'Penguin,' Commander W. U. Moore.*

By R. I. Pocock, of the British (Nat. Hist.) Museum.

[Plate XX. B.]

During the past two years the Trustees of the British Museum have received from the Lords of the Admiralty an immense and very valuable series of Crustacea obtained by Mr. P. W. Basset-Smith, of H.M.S. 'Penguin,' in the Australian and China Seas.

The Stomatopoda alone of this series form the subject of the present communication; but it is probable that when the rest of the material is examined, the remainder of the orders will be found to be equally well represented by new and interesting forms.

I may add that, during a recent visit to the British Museum, Dr. H. J. Hansen, of Copenhagen, made a thorough revision of our extensive collection of Squillidæ. Amongst other important innovations, Dr. Hansen has suggested more than one new generic name for certain species that have been hitherto referred to previously existing genera; but until he has himself published the descriptions of these genera, I have not considered it advisable to adopt them.

(1) *Squilla fasciata*, De Haan.

Two specimens. Chusan (10–14 fath.); Holothuria Bank (34–36 fath.).